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Tabwecala robinsoni gen. nov., sp. nov., from Vanuatu and its systematic position in the 'Ophiusini-Poaphilini' clade (Lepidoptera, Erebidae)

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Abstract. A new erebid, *Tabwecala robinsoni* **gen. nov.**, **sp. nov.**, from the Vanuatu Islands (Espiritu Santo) (West Pacific Ocean) is described. The new species, superficially resembling species of the genera *Artena*, *Achaea* or *Leistera*, shows a peculiar combination of characters which suggested its placement in a new genus. This is provisionally placed in tribe Poaphilini but following a review of the features purporting to show the separation of Ophiusini and Poaphilini, it is shown that morphological rationale supporting the current arrangement of these tribes is still lacking. Noteworthy modifications affect the hindleg of male *Tabwecala robinsoni*, with greatly shortened and swollen metatibia bearing a dorsal hair-pencil.

Introduction

Following an analysis of the macrolepidoptera of the archipelago of Vanuatu (formerly known as New Hebrides), Robinson (1976) recorded 29% of the species as endemic (105/364). However, based on the relatively young age of the islands and because, compared to e.g. New Caledonia and Fiji, no groups showed radiation into species complexes, he concluded that the moth fauna of Vanuatu was "recent and derived solely by transoceanic dispersal". It is also worth noting that only one endemic (and undescribed) genus from Vanuatu was known to Robinson (1976), which may be taken as a proxy of low overall morphological diversification in the islands and hence as additional evidence for their comparatively recent faunal settlement. Substantially similar figures can be drawn from Bradley's (1962) review of the microlepidoptera from Aneityum, Vanuatu's southernmost island, with 26% endemic species (18/69) and no endemic genus. Some endemic genera from the archipelago had indeed been described by Meyrick (1906, 1924), notably *Loxotrochis* Meyrick, 1906 (Immidae) and *Hedroxena* Meyrick, 1924 (Cosmopterigidae), but the former had very soon been shown to be based on a misreading of the locality of Espirito Santo (Brazil) as Espiritu Santo (Vanuatu) (Meyrick 1907), although this emendation has sometimes been overlooked (e.g., Viette 1949). Numerous new endemic species have since been discovered in Vanuatu, especially by Holloway (1979) but also by other scholars, who even spotted large-sized colourful butterflies and moths such as *Polyura sacco* Smart, 1977 (Nymphalidae), *Gnathothlibus saccoi* Lachlan & Moulds, 2001, *G. vanuatuensis* Lachlan & Moulds, 2003 (Sphingidae) and *Eudocima oliveri* Zilli & Brou, 2017 (Erebidae) (Smart 1977; Lachlan and Moulds 2001, 2003; Zilli et al. 2017). It is thus easy to assume that these islands still host several lepidopterological treasures, whose discovery will benefit from studying expedition collections from

the archipelago. As usual, most research on the Lepidoptera from Vanuatu has been dedicated to butterflies (e.g., Butler 1875; Gross 1975; Tennent 2004, 2006, 2009), while only two main surveys have targeted moths. The first was Robinson's, during a Royal Society/Percy Sladen Trust expedition in 1971. The other took place in 2006 as part of an IBISCA ("Investigating the BIodiversity of Soil and CAnopy") project focused onto the island of Espiritu Santo. The full results of the two surveys have not been published, although syntheses appeared in Robinson (1976), Holloway (1979), during a zoogeographical comparison of Robinson's data with the fauna of New Caledonia, and Kitching (2011), reporting on the results of the IBISCA-Santo expedition. Robinson (1975), however, provided a list of preliminarily identified species from Vanuatu in his monograph on Fijian moths, but some material was left unstudied. This material is available at the Natural History Museum of London and its study already yielded the new species of *Eudocima* Billberg, 1820 mentioned above. This contribution reports on the discovery of another endemic erebid moth during Robinson's expedition, which is described here, and probably represents the new genus briefly mentioned by him in 1976. In fact, due to its unusual features, the erection of a new genus to accommodate the new species becomes necessary.

Material and methods

Study material originated from the expedition by G.S. Robinson to the New Hebrides in 1971 preserved in the Natural History Museum of London (**NHMUK**). Photographs and dissections were performed according to the procedure already outlined in Zilli (2020), with minor updates of software for operating the camera (Helicon Remote version 3.9.12), image stacking (Helicon Focus vers. 7.5.8) and processing (Adobe Photoshop 2021 vers. 22.3.1). As in numerous erebid groups, the female abdominal sternum A7 is strongly modified in the new species and gives rise to a so-called lodix plate (Goater et al. 2003). This is tightly joined with the ostium bursae but, with some care, a tiny membrane between the two can be cut with microsurgical scissors, which was done to reveal the real configuration of the ostium bursae and, as in this case, the sterigma. Legs and proboscides were prepared following the same dissection and mounting methods as the genitalia. Pictures of forewing veins were taken after partial descaling of the wing disc undersides following wetting of the wing membrane with absolute ethanol. Terminology of veins is mainly based on Wootton (1979) and Kristensen (2003). However, assessment of the homologies between two strikingly different intraspecific configurations of the forewing radials that have been observed was found to be affected by what sections are considered to constitute the chorda, especially as regards the distal closure of the areole. Accordingly, the branching pattern from the areole is reported in two ways, a purely descriptive one, in which the areole is considered as a term of reference, and an interpretative one to better express the relationships between the observed patterns. The latter takes the cell as term of reference and incorporates modifications of convenience to make clearer if the branch of a vein precedes (') or follows (") a cojoined section with other veins.

Results

Taxonomy

Tabwecala gen. nov.

http://zoobank.org/F744DF74-AE2D-4236-8089-076C74D3EB81

Type species. *Tabwecala robinsoni* sp. nov. (described below), by present designation.

Etymology. The generic epithet derives from the combination of "Tabwe-" (from Mt Tabwemasana in Espiritu Santo Island) and "-cala" (from the Greek "κᾰλή", meaning "nice"); it is feminine in gender.

Diagnosis. The absence of sexual dimorphism in the labial palpi, the presence of two anterior spines on the male profemur, the absence of spines on male tibiae, the presence of an androteca on male mesotibia, the strongly modified male metatibia bearing a dorsal hair pencil, the tuba analis without scaphium and with a deep, hood-like scaphial pocket, and the sterigma projected posteriorly into a free end, represent altogether a combination of characters not seen, at the author's best knowledge, in other genera of the Erebidae.

Description. Male (Fig. 1). ***Head.*** Large, feebly sunk into thorax, frons slightly bulged, unscaled at middle (scales evidently brushed off by labial palps after emergence as in numerous other Erebinae), vertex roughly scaled, eye large, globular, antenna filiform, scape stout, barrel-like, covered by scales projected into small dorsal hood, pedicel small globular, flagellum consisting of short cylindrical, ventrally very shortly ciliate antennomeres, pilifer conspicuous, with long bristles, haustellum well developed, with tiny flat apical sensilla, labial palpus slender, upcurved, first joint roughly scaled, second joint compactly scaled, third joint long and thin, rod-like, two thirds as long as second, with no apical club.

Thorax. Stout, both patagium and tegula broad and long, roughly scaled, meso-metanotum with hair-like scales, without crests; pectus conspicuously hairy. Wings broad; forewing vein R1 from middle of cell, areole present, splitting between Rs_2 and Rs_3 close to termen in apical area of wing, but topology of Rs branches from cell very variable (see dedicated paragraph below), M visible in outer half of cell, other veins as in other Erebinae, with CuA_2 from before middle of cell; hindwing veins as in other Erebinae. Legs slender (Fig. 3); foreleg: profemur elongated, slightly wider at base and gradually tapered distally, with paired preapical spines, protibia not spined, barely shorter than femur, and feebly incrassate at middle, with epiphysis half length of tibia, protarsus conspicuously spined ventrally on tarsomeres I–IV, spines arranged into 3 rows, terminal spines of each tarsomere longest, spines replaced by bristles on tarsomere V, pretarsus with semi-circular arolium, onychia sharply bent, with midventral tooth, and pulvilli short; midleg: longest of the three legs, mesofemur long and slender, of almost uniform width, mesotibia greatly developed, longer and wider than mesofemur, its edges wrapping internally so as to originate a groove (androteca, cf. Berio 1955, 1959, 1965) enclosing a long hair-pencil kept in place by flat scales, mesotibial spurs one terminal pair, mesotarsus slender, spines and bristles on I–V as in protarsus, pretarsus as in protarsus; hindleg: metafemur slender and of almost uniform width, 7/10 as long as mesofemur, metatibia not spined and greatly modified, very short, about 2/3 length of metafemur, and swollen distally and dorsally so as to show a teardrop outline with dorso-apical bulge (respecting tibio-tarsal axis) for insertion of conspicuous pencil of long, hair-like androconial scales, this leaning middorsally along basal tarsomere, metatibial spurs two pairs, long and flimsy, first pair from middle of metatibia, second pair from well before apex, mesotarsus with basal tarsomere greatly developed, thick and longer than tarsomeres II–V altogether, widest at base and gradually tapered apically, clothed externally with thin long setae and showing midventrally in its distal two thirds comb of long bristles, tarsomeres II–V and pretarsus as in fore- and midleg.

Abdomen. Sternum A2 broad, subrectangular, with short, broad-based anterior apodemes, other segments of pregenital abdomen with subrectangular urotergites and urosternites, much wider than high, tergum A8 trapezoid, sternum A8 shallowly cleft on its posterior margin.

Male genitalia (Fig. 5). Tegumen and vinculum robust, the latter shorter than tegumen and without inwardly produced saccus, valva oblong, with strongly sclerotised proximo-ventral portion, deriving from fusion between costal process and clasper, narrowly joined to sacculus, this produced into short saccular process, and dorso-distal membranous portion, which is broadly but shallowly corematous dorsally at base, where a conspicuous scent tuft is inserted. Uncus with dorsal process far from base. Tuba analis of complex configuration, dorsally membranous, showing distinct hood-like scaphial pocket (best seen in side view) above anus to accommodate tip of uncus. Juxta long, symmetrical, of the 'X'-type, articulated at very base of valvae. Phallus arched and compressed, with recurved foot-shaped coecum, showing small sclerotised platelet at base of vesica in distal excision of ventral edge of its shaft, vesica multi-lobed.

Female (Fig. 2). ***Head.*** As in male, no sexual dimorphism detectable, including labial palpus, except for base of flagellum, slightly thinner, and periscapular scales, shorter and not forming hood.

Thorax. Pro-metathorax and wings as in male, legs without the sexual secondary modifications seen in male (namely, profemural spines, mesotibial androteca, shortened and swollen metatibia bearing dorsal scent pencil and weak spurs, strongly developed basal segment of metatarsus with setae and comb), mesotibia irregularly spined externally, metatibia not spined, basal segment of metatarsus as long as tarsomeres II+III, with three rows of spines ventrally (Fig. 4); other features as in male.

Abdomen. As in male but tergum A7 broad and high, approximately square-shaped, and sternum A7 greatly reduced to narrow and long subrectangular lodix plate (Fig. 6) overlapping ostium bursae.

Female genitalia (Fig. 6). Complete sterigma present and of complex configuration, corresponding to broadly dilated midventral section of intersegmental membrane A7–A8 produced midventrally into stout, strongly sclerotised longitudinal outgrowth that terminates posteriorly into free end overlapping midventral sclerotisation which extends between from post-sterigmatal area to sternum A8; ostium bursae opening at approximately one third from anterior margin of sterigma. Bursa copulatrix with broad cervix and appendix anteriorly oriented originating from left of this. Ovipositor short, papillae anales soft, elongated, densely setose. Gonapophyses rod-like.

Venational variation. Two different configurations regarding topology of forewing Rs veins, not linked to the sexes of specimens examined, have been found. As noted in the 'materials and methods', these are reported here after a descriptive approach (italics between brackets) and an interpretative one (normal text and Figs 7, 8).

(1) [*Areole long; Rs_1 from just beyond middle of areole; Rs_2 and Rs_3 long stalked, from upper distal corner of areole; Rs_4 from lower distal corner of cell*] Rs_1 and stalk (Rs_2+Rs_3) long stalked, from before end of cell, areole very long, bound superiorly by stalk (Rs_1+(Rs_2+Rs_3)) and stalk (Rs_2+Rs_3), inferiorly by Rs (viz. cell) and Rs_4, and closed by short anastomosis that from Rs_4 reaches stalk (Rs_2+Rs_3) (Fig. 7).

(2) [*Areole short; Rs_1 from 4/5 length of areole; stalk of Rs_2 and Rs_3 shortly stalked with Rs_4, from end of areole*] Rs_1 and Rs_2' stalked, from before end of cell, Rs_2' free from bifurcation with Rs1 for short tract, then anastomosed and cojoined into short stalk ((Rs_2"+Rs_3)+Rs_4") which then separates into long stalk (Rs_2"+Rs_3) and Rs_4", areole thus short, bound superiorly by stalk (Rs_1+Rs_2') and Rs_2', and inferiorly by Rs (viz. cell) and Rs_4' (Fig. 8).

Figures 1, 2. Habitus of *Tabwecala robinsoni* gen. nov., sp. nov., from Vanuatu, Espiritu Santo, Mt Tabwemasana. **1.** Holotype ♂; **2.** Paratype ♀. Scale bar: 1 cm (**1, 2.**).

Distribution. The genus is currently known only from a restricted area of the Pacific (Vanuatu: Espiritu Santo).

Systematic position. Features of the new genus indicate its position in tribe Poaphilini of the Erebinae (Erebidae), a group which is however morphologically ill-defined, as it will be reviewed in the discussion below.

Tabwecala robinsoni sp. nov.

http://zoobank.org/A6832F40-B17C-498D-B714-6B9217405BB6

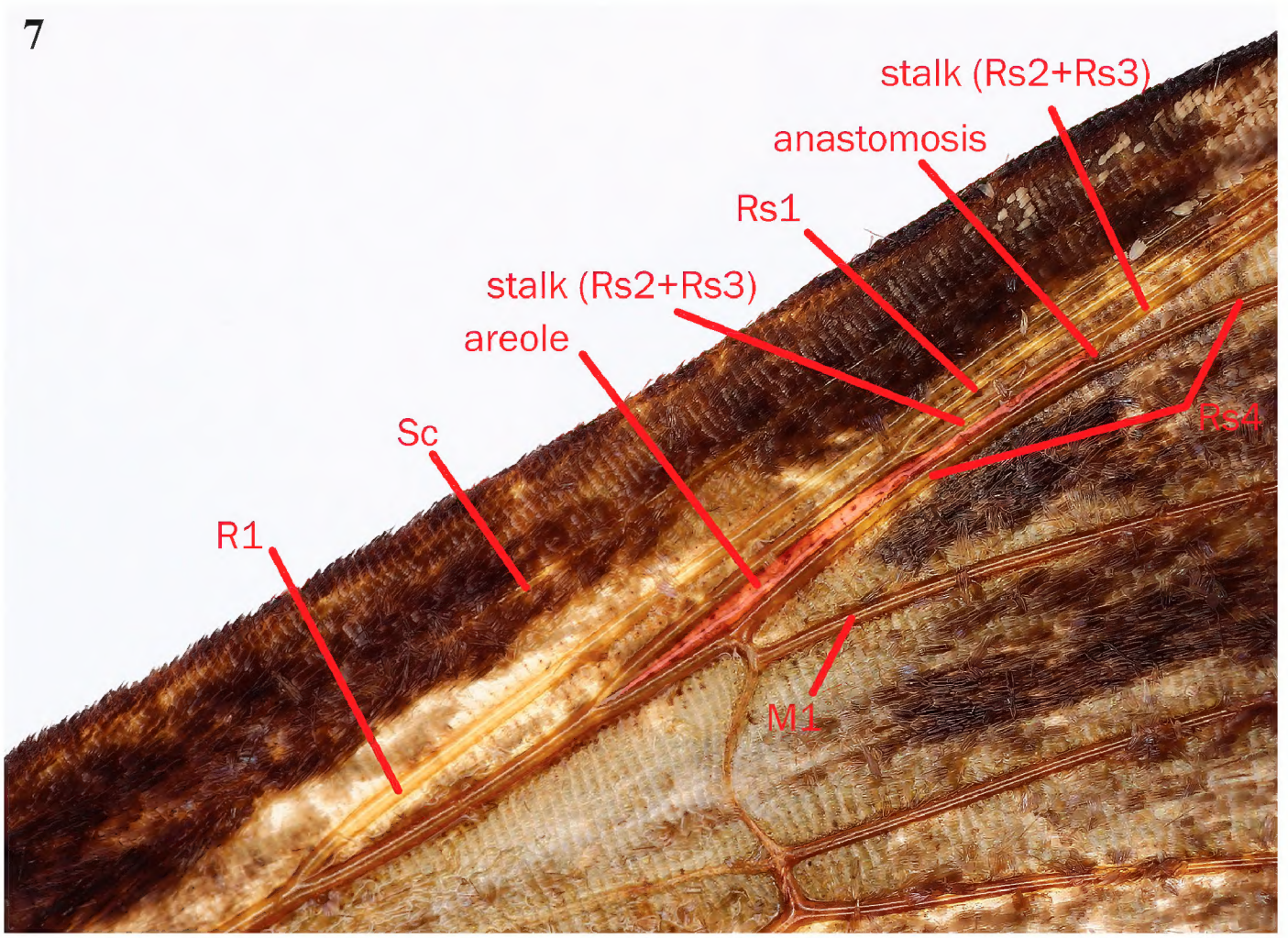
Type material. ***Holotype*:** VANUATU • ♂; "New Hebrides", [Espiritu] Santo, Mt Tabwemasana Ridge; alt. 1372 m; 2 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010354772; NHMUK. ***Paratypes*** (3♂♂, 5♀♀)**:** VANUATU • ♂; same data as for holotype; NHMUK010918854; NHMUK • ♂; same data as for holotype; NHMUK010918855; NHMUK • ♀; same data as for holotype; NHMUK010354773; NHMUK • ♀; same data as for holotype; NHMUK010918853; NHMUK • ♂; Mt Tabwemasana, Nokowula; alt. 1128 m; 1 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010354774; NHMUK • ♀; same data as for preceding; NHMUK010918633; NHMUK • ♀; same data as for preceding; NHMUK010918636; NHMUK • ♀; same locality as for preceding; alt. "CK-" 1067 m; 3–4 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010918856; NHMUK.

Etymology. The species is dedicated to the memory of the collector of the type series Gaden S. Robinson (1949–2009), former researcher and curator of Lepidoptera at the then British Museum (Natural History). The specific epithet is a noun in the genitive case.

Diagnosis. The new species looks superficially similar to species of the ophiusine genus *Artena* Walker, 1858, especially members of *Artena rubida*-group, namely *A. reggiantii* Zilli & Lourens, 2018, *A. velutina* (L.B. Prout, 1919) and *A. rubida* (Walker, [1863]), but is easily recognisable by the non-sexually dimorphic, slender rod-like third joints of labial palpi, rough instead of plain scaling of head and thorax, uniformly dark-coloured forewing without pale antemarginal field, larger, more centrally- and transversely positioned pale band of the hindwing and conspicuous scent tufts on the upperside of male metatibiae. Also somewhat resembling in habitus members of the poaphiline genus *Achaea* Hübner, 1823 and the yet incertae sedis genus *Leistera* Swinhoe, 1909, the latter showing another unusual combination of characters (type species, *Catephia pulchristrigata* Bethune-Baker, 1906, examined), e.g. no androteca as in Catephiini (Berio 1992) but unlike these with spines on male meso- (weakly) and metatibiae, uncus with dorsal peak and valva structured as in several members of the Ophiusini + Poaphilini clade, including also single tubular

Figures 3, 4. Legs of *Tabwecala robinsoni* gen. nov., sp. nov. **3.** Male; **4.** Female (this also with procoxa). Scale bar: 2 mm. (**3, 4.**)

Figures 5, 6. Genitalia of *Tabwecala robinsoni* gen. nov., sp. nov. **5.** Male, paratype; **6.** Female, paratype (sternum A7 on left). Scale bar: 1 mm (**5, 6.**).



Figures 7, 8. *Tabwecala robinsoni* gen. nov., sp. nov., different branching patterns of veins from forewing areole (shaded light red) with interpretation of homologies (see criteria in Material and methods). **7.** Long-areoled configuration; **8.** Short-areoled configuration; **M** – medial; **R** – radial; **Rs** – radial sector; **Sc** – subcostal. Scale bar: 1 mm (**7, 8.**).

dorsal corema from its base. Nonetheless, no *Achaea* species with forewing completely deprived of pattern are known to date, and the arabesqued ornamentation of forewing of species of *Leistera* will prevent any confusion.

Description. Male (Fig. 1). ***Habitus.*** Wingspan 74.5–78 mm (mean = 76 mm, n = 4). Ground colour of head, body trunk and forewing uniformly dark blackish brown, with some scattered sprinkles of silvery scales. Forewing broad subtriangular with no evident pattern, apex smoothly rounded, termen overall slightly convex, feebly undulated at veins, anal margin straight, fringe concolorous with wing disc; hindwing broad and rounded, termen as in forewing but slightly produced at vein 1A+2A and with feeble white terminal line, colour dark chocolate brown, except for broad transverse white discal band, this widest at middle and with margins blurred, and with very feeble light-blue hue (visible if swinging the wing), ending before anal margin. Metatibial scent pencil blunt-ended and reaching in length almost the whole basal tarsomere, its basal third chocolate brown-coloured, mesially and distally brightly honey-coloured. Underside almost unicolorous dark blackish brown.

Male genitalia (Fig. 5). Tegumen high, very tapered superiorly, with small thorn-like projections before apex; vinculum semicircular; valva oblong-obovate, with hairy distal membranous section, sacculus small, lozenge-shaped, with small apical outwardly-produced horn-like process, ventral sclerotised part centrally positioned, in shape of wide-based sub-rectangular transverse plate ending distally into two processes, inferior one (interpreted here as a clasper proper) thumb-like, perpendicular to longitudinal axis of valva, and superior one (interpreted as of costal derivation) similarly shaped but longer and much stouter, subparallel to costal margin, with reclinate tip, inflatable saccate corema on dorsal side with thick tuft of long hair-like scales; uncus long and reclinate, bulbous at base, its dorsal process subbasal and horn-like with forward projected tip, distally sinuous with middorsal hump and downcurved pointed tip; tuba analis wholly membranous. Juxta narrow, sub-rectangular, slightly sinuous at sides, with slightly divergent projections at corners, the inferior pair articulated with valvae. Phallus bent at basal third, vesica small, with paired opposite long thin diverticula and central, slightly bilobed bulge protruding from central corpus.

Female (Fig. 2). ***Habitus.*** Wingspan 71.5–77.5 mm (x = 75.6 mm, N = 5). As in male, except for legs (described under generic diagnosis), and with white band of hindwing wider at middle of wing disc. Sternum A7 (lodix) posteriorly bilobate (Fig. 6).

Female genitalia (Fig. 6). Tergum A8 wide and short, its ventro-lateral belts facing the sternum about half as high as the dorsal part, long and with rounded ends, separated only by narrow sternal section, apophyses anteriores thin; basal sterigmatal plate broad and rugulose, trapezoid, its ventral longitudinal outgrowth narrow, sub-rectangular, posteriorly bifid with conspicuous, pointed asymmetrical processes, and with anterior excision extending posteriorly as a narrow furrow for about one third of its whole length, ostium bursae opening at bottom of short infundibular depression in correspondence of posterior end of midventral furrow, sternum A8 with narrow elongated sclerotisation proceeding from post-sterigmatal area. Ductus bursae very short, strongly sclerotised, joining with corpus bursae at junction between broad, dome-shaped cervix, which thus extends posteriorly to it, and large ovoid fundus bursae (note that the several irregular dark blotches visible in fig. 6 appear in completely other positions in another preparation, thus they seem tissue remains not pertaining to the bursa, though they appear tightly linked to it and not separable in the well cleaned preparations); appendix bursae conical. Intersegmental membrane A8–A9 short. Papillae anales elongated sub-rectangular, apophyses posteriores approximately 1.5 times as long as anteriores.

Distribution. Currently known only from the island of Espiritu Santo in the Vanuatu archipelago.

Bionomics. The original series was collected in a period of four days on the Mt Tabwemasana range, the highest peak of the island of Espiritu Santo and whole Vanuatu archipelago, at elevations between 1067 and 1372 m, which correspond to sites of *Agathis-Calophyllum* and montane cloud forests (Munzinger et al. 2011).

Discussion

Tabwecala robinsoni shows features which agree with what is nowadays mostly referred to as the Ophiusini + Poaphilini clade (e.g., Homziak et al. 2019). The concept of Ophiusini, historically revised many times (Kitching 1981; Kühne and Speidel 2004; Homziak et al. 2016), has recently been split between the tribes Ophiusini and Poaphilini (Lafontaine and Schmidt 2010, 2013; Zahiri et al. 2012), the latter being revived from Euclidiini, mainly based on molecular evidence. In the analyses by Zahiri et al. (2012), confirmed also by Homziak et al. (2019), each group has been recovered as monophyletic with good support but also as sister to the other in a well-supported clade, which raises the issue whether splitting them taxonomically was strictly necessary. Further to this, there are no known autapomorphies supporting the separation of the two tribes.

Zahiri et al. (2012) mention for the Ophiusini that "*Ophiusa*, *Thyas* and *Artena* all have a strongly modified apex to the proboscis, with strong and enlarged spines and erectile, reversed hooks that are used in fruit-piercing or lachrymal-feeding behaviour". Such statement, attributed to Holloway (2005), was evidently a lapsus for the Calpinae (or Calpini), the erectile reversed hooks being a well-known character exclusively occurring in Calpinae/i (Speidel et al. 1996; Kitching and Rawlins 1998; Zaspel et al. 2011). In fact, Holloway (2005: 11) noted that the three genera have only enlarged spines and that these were not erectile like those of the Pericymini, and stated that strongly sclerotised, erectile, reversed hooks occur instead in Calpini and Scoliopterygini. During the present study, it was decided to compare the structure of the proboscis of *Artena* (*A. dotata* Fabricius, 1794, examined) and *Achaea* (*A. serva* Fabricius, 1775, examined), genera attributed respectively to Ophiusini and Poaphilini (Zahiri et al. 2012). No tearing hooks were observed. In contrast, the same basic structure was detected, both taxa showing only thin, nail-like spines and other sensilla in the apical section of proboscis. The fruit-piercing behaviour does not allow the separation of the two groups either, as also noted by Zahiri et al. (2012), since it has been recorded by Bänziger (1982) both in genera of the restricted Ophiusini (e.g., *Artena*, *Ophiusa*, *Thyas*) and others now placed in Poaphilini (e.g., *Achaea*, *Ophisma*, *Bastilla*, *Grammodes*) (Zahiri et al. 2012; Lafontaine and Schmidt 2013). In relation to lacriphagy, Bänziger (1973) summarised all data known to date and neither recorded Ophiusini nor Poaphilini. These results are in full agreement with Bänziger's (2021: 139–140) independent review of the issue just published.

Homziak et al. (2016), in their historical review of the classification of the Erebinae, noted the treatment of Ophiusini and Poaphilini by most recent authors but also that early authors did not separate them, and often recorded features shared or scattered across taxa that are currently separated into the two groups. They noted that the restricted concept of Ophiusini matches the section comprising *Artena*, *Ophiusa* Ochsenheimer, 1816 and *Thyas* Hübner, 1824 that was circumscribed by Holloway (2005) on basis of absence or strong reduction of dorsal valval coremata and absence of a powdery or waxy bloom on the pupa. Holloway had also mentioned a dorsal elliptical mark on larval A5 uniting *Artena* and *Thyas*, but its absence in other Ophiusini such as *Ophiusa* and *Clytie*

Hübner, 1823 (cf. Leong 2009; Herbison-Evans and Crossley 2021; Mazzei et al. 2021) excludes this feature from the list of putative synapomorphies.

As regards the valval coremata, *Artena* lacks them, in *Ophiusa* they are generally shallow (Holloway 2005), but those of *O. trapezium* (Guenée, 1852) are bigger than those of a poaphiline species such as *Ophisma gravata* Guenée, 1852 (cf. Holloway 1979; and pers. obs.), and the ophiusine *Stenopis reducta* Mabille, 1880 has long tubular coremata (De Prins and De Prins 2011–2021) not dissimilar from those of some Poaphilini in the so-called *Parallelia*-complex like *Pindara* Moore, [1885] or *Macaldenia* Moore, [1885] (cf. Holloway and Miller 2003; Holloway 2005). Splitting the two groups on this character looks therefore untenable. More promising seemed to be the character of the bloom on pupae, widespread in the Erebinae but apparently absent in the Ophiusini, so that its loss could have served as an autapomorphy delimiting the restricted concept of this tribe. Nonetheless, good illustrations of pupae of *Ophiusa disjungens* (Walker, 1858) and, particularly, *Thyas coronata* (Fabricius, 1775) clearly show that a pupal bloom also occurs in some species of this group, the pupa of the latter being also explicitly stated to be "covered in a white waxy powder" (Herbison-Evans and Crossley 2021).

A further character which has been used to unite the modern Ophiusini is the similarity in pattern, though considering the range of patterns expressed by genera of the Ophiusini and Poaphilini the overall picture is so intermingled that it is debatable that a phylogenetic signal may be traced here. *Tabwecala* itself, which in leg features corresponds to Poaphilini (see description above and comments below), shows the greatest similarity in external appearance to species of *Artena* (Ophiusini), especially members of the *A. rubida* group (cf. Zilli and Hogenes 2004; Zilli and Lourens 2011). Solely upon basis of the habitus it had provisionally been marked by Gaden S. Robinson with "Closest ally Artena rubida Walk.".

Emphasis has also been laid on the widespread acceptance of Euphorbiaceae as hostplants by members of the Poaphilini (Holloway and Miller 2003; Homziak et al. 2016). The host range of Poaphilini is wide in terms of plant families and many overlaps occur with the Ophiusini. Following a recent analysis run on the hostplant data of Robinson et al. (2001), Holloway (2019 and pers. comm.) notes that of the 15 families exploited by the Ophiusini in the Indo-Australian Region, eight are shared with the Poaphilini, while the latter feed on a range of at least 35 plant families (Phyllanthaceae being then still subsumed into the Euphorbiaceae), though the Euphorbiaceae take the lead. This feature seems therefore quite well embedded into the poaphiline lineage, especially in the *Parallelia*-complex studied by Holloway and Miller (2003). However, (A) the existence of several poaphilines feeding on other plant families or at least not known to feed on Euphorbiaceae, (B) the diffuse polyphagy by some species which also exploit euphorbs (Robinson et al. 2001, 2021; Holloway and Miller 2003) and (C) the varying rate of their acceptance, indicate that such habit has to be better considered as a 'syndrome' rather than a synapomorphy uniting the whole Poaphilini. For example, out of 35 hostplant associations recently recorded by Staude et al. (2020) for *Achaea* in South Africa, 34.3% were Fabaceae, 14.3% Anacardiaceae, 8.6% each Combretaceae and Rhamnaceae, 5.7% each Myrtaceae, Ochnaceae and Zygophyllaceae, and only 2.9% each (1 record) Euphorbiaceae, Malvaceae, Phyllanthaceae, Plumbaginaceae, Sapindaceae and Sapotaceae. Euphorbs are also known to enter the larval diet of many genera of Erebinae outside of the Ophiusini + Poaphilini clade, e.g. *Asota* Hübner, [1819], *Cosmophila* Boisduval, 1833, *Homodes* Guenée, 1852, *Hypocala* Guenée, 1852, *Tamba* Hübner, [1823], *Ugia* Walker, 1858 (cf. Robinson et al. 2021), thus also this feature appears to be a symplesiomorphy. There is also an indication that

Ophiusa sp. may feed on *Hevea brasiliensis* Müll. Arg. (Euphorbiaceae) in Malaysia (Robinson et al. 2001, 2021; Holloway 2019 and pers. comm.), though such records are drawn from a time when the use of this generic concept among applied entomologists may have been different from the current one (e.g., Rao 1965), even comprising poaphiline taxa such as members of *Achaea*. For instance, *A. janata* (Linnaeus, 1758) (= *melicerta* Drury, [1773]), highly polyphagous and especially feeding on Euphorbiaceae, has long been recorded in the past under *Ophiusa* (e.g., Ridley 1904; Lefroy 1908; cf. Waterhouse 1993).

Apparently good characters to differentiate between the two groups remain those outlined by Berio (1959, 1965) for his 'phyla' of *Anua* (= Ophiusini) and *Achaea* (= Poaphilini), both having from one to three spines on the male forefemur (Homziak et al. 2016 record four in Poaphilini but this also seems a lapsus), but differing in the position of the androteca, on the profemur and mesotibia, respectively. For this reason, the systematic position of *Tabwecala*, with its typical mesotibial androteca, is here considered to be in the Poaphilini. However, even if these characters have a diagnostic role, they are unsuitable in the delimitation of either tribe, being symplesiomorphies shared with other erebine groups. A mesotibial androteca is also typical of the Catocalini and Pericymini (Berio 1959: 289; Kühne 2005: 34), and it cannot therefore be used to circumscribe the Poaphilini, while the proleg type is also found in *Audea* Walker, [1858] and *Crypsotidia* Rothschild, 1901 (Audeini) (Berio 1959; Kühne 2005). *Ulotrichopus* Wallengren, 1860 (Catocalini) may have both types (Kühne 2005, and pers. obs.), in some species (*U. variegata* Hampson, 1902, examined) even showing an unusually oriented bunch of modified setae which overlap from the trochanter onto the femur as in some Ophiusini, e.g. *Ophiusa tirhaca* (Cramer, [1777]) (examined), *O. dilecta* Walker, 1865 and *Stenopis tumiditermina* (Hampson, 1910) (cf. Berio 1965).

There are several other characters uniting the Ophiusini and Poaphilini. They all have membranous papillae anales without sclerotised strips following up in line with the apophyses posteriores, this being a feature of Catocalini, Audeini and Catephiini (Mitter and Silverfine 1988; Goater et al. 2003; Holloway 2005; Kühne 2005; Homziak et al. 2016), and many species of genera of the two tribes sport a dorsal peak or process on the uncus (= superuncus *sensu auct. nec* Klots, 1956), e.g. *Artena*, *Ophiusa*, *Clytie* (Ophiusini) and *Achaea*, *Ophisma* and *Bastilla* Swinhoe, 1918 (Poaphilini). Similarly, many members of the two groups show the coecum of phallus dorsally upcurved into a 'foot-shape', and a basically similar structure of the valva (cf. Berio 1965; Holloway and Miller 2003; Holloway 2005). A broader taxon sampling has therefore to be recommended in future molecular analyses to better refine the relationships within the Ophiusini + Poaphilini clade, the two groups possibly not deserving to be split taxonomically in consideration of the absence of clear autapomorphies supporting each individual group and the molecular evidence corroborating their status of adelphotaxa. In this respect, molecular analysis of taxa showing unusual combinations of characters such as *Tabwecala* would be a priority. Besides the features the new genus has in common with several members of both branches of the Ophiusini + Poaphilini clade, such as the corematous valvae, dorsal process of uncus and upcurved coecum, it also shows traits that are found only in one of the two 'tribes', such as a mesotibial androteca (Poaphilini). The subbasal rather than basal dorsal process of the uncus is instead a feature more typical of certain Ophiusini such as *Clytie*, with which *Tabwecala* also shares a remarkable similarity in the main part of the structure.

Most notable are the exclusive features of the new genus. The absence of the dorsal sclerotization of the tuba analis (scaphium) occurs sporadically in the Erebidae. Following the union with the then families of Arctiidae and Lymantriidae based on molecular evidence (cf. Mitchell et al.

2006; Zahiri et al. 2011), the importance of the scaphium as an autapomorphy characteristic of the Erebidae (cf. Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006) has been devalued. It may also be present or not within the same infrafamilial grouping. Examples are in the Toxocampinae, species of the *Autophila* group showing a scaphium but not so those of the *Lygephila* group (cf. Ronkay et al. 2014; Pekarsky et al. 2019), or the Omopterini *Zale* Hübner, 1818 and *Matigramma* Grote, 1872, scaphium present and absent, respectively (cf. Blanchard and Franclemont 1982; Franclemont 1986). However, the absence is yet unrecorded in the modern concept of Ophiusini and the Ophiusini + Poaphilini clade, which typically sport a scaphium. In species with a dorsal process of the uncus it even contributes to the characteristic 'triple beak topping' of the male genitalia common to many members of the clade. Possibly related to this is the development in *Tabwecala* of a hood-like invagination in the superior part of the tuba analis to form a large scaphial pocket that wraps the tip of uncus to likely prevent damages to the rectum. This configuration is more similar to that of the distantly related Hypeninae than to the small rugulose invagination distal to the scaphium, essentially serving the same function, that occurs in Calpinae and other Erebinae (cf. Lödl 2000; Goater et al. 2003).

Legs of *Tabwecala* offer a plethora of unusual features, starting from the distribution of spines on tibiae. The combination of "♂:000; ♀:010" (where 0/1 = absence/presence in pro-, meso- and metatibia, respectively), that corresponds to Berio's (1959, 1965, 1992) grade VII of spinosity, has not been recorded by Berio in any ophiusine or poaphiline. Berio did not record in all Erebinae he studied any grade VII species with male profemural spine(s) like instead *Tabwecala* has. The remarkably short, teardrop-shaped male metatibiae bearing a dorsal scent pencil oriented posteriorly are unique, possibly in the whole Erebidae. Noteworthy modifications in male metatibiae to support a scent function are known in other erebids, e.g. *Ascalapha* Hübner, [1809] (Müller 1877; Barth 1951), but their configuration is totally different from that of *Tabwecala*.

In the female, the sterigma surrounding the ostium bursae that projects ventrally and posteriorly into a free lamella and the simultaneous presence of a post-ostial midventral sclerotization from intersegmental membrane A7–A8 to sternum A8, so that technically the new species shows two "lamellae postvaginales", is also unusual but reviewing details of this area in the specialised literature is difficult because of the practice of not removing sternum A7 (lodix) during preparation of the female genitalia.

Regarding the remarkable variation in wing venation shown by *Tabwecala*, little can be said other than confirming that topology of veins should be always carefully checked on more specimens. Venational patterns were very much used in the past for systematic purposes, but their value has greatly been downscaled (Kristensen 2003), also in the light of remarkable intraspecific variability. This was long known to be common in the more basal lepidopteran lineages but is has also been shown to occur in the most derived families (Alberti 1954; Sotavalta 1964; Albrechts and Kaila 1997; Nath and Sevi 2009), venational patterns being subject during morphogenesis to many regulatory mechanisms that can modulate expression (cf. Shimmi et al. 2014). Nonetheless, topology of wing venation still remains much employed in systematics (e.g., Souza Moraes et al. 2021).

Conclusions

The discovery in a wildlife sanctuary such as the montane forests of the Tabwemasana range in Espiritu Santo (Vanuatu archipelago) of a new species of Erebidae that could not be systematically

placed into any genus known to date shows how partial our knowledge about the diversity of one of the richest families of Lepidoptera remains. Such diversity is not just in terms of species, but also involves genes, morphological traits and eco-ethological adaptations, like those represented by the leg modifications of male *Tabwecala* and their likely role in scent emission and in courtship. The scent organ shown by *Tabwecala* also raises issues about the evolutionary context behind such innovation, given that this insular endemic has a systematically and biogeographically fairly isolated position, so that it does not seem to face any risk of mating mistakes with sympatric relatives. The male scent apparatus seems therefore not to have evolved to promote a species isolating role from any close allies but to enhance the recognition and synchronization of the two sexes in an insular context (cf. Zilli 1993, for a discussion on alternative hypotheses).

Pointing to areas where to look for putative relatives of *Tabwecala* is highly speculative. On the one hand, following an analysis of a major database of plant generic distributions, the tightest phytogeographical links of Vanuatu have been found with eastern archipelagos such as Samoa, Fiji and Tonga (Holloway 1979: 44), locations where no similar groups to the new genus have been found. On the other hand, the geographical range of numerous Lepidoptera species pertaining to the so-called New Caledonian and Fijian elements place the Vanuatu at the crossroads between those two distribution patterns (Holloway 1979). The New Caledonian Lepidoptera have extensively been surveyed, but the moth faunas of the Solomon and Bismarck archipelagos, that is the most western islands comprised within the New Caledonian element (Holloway 1979), still require proper insights and might reveal groups linking to *Tabwecala*.

Interestingly, the most endemic lepidopteran fauna of Vanuatu is from the island of Espiritu Santo, e.g. there are 33 single island endemic macrolepidoptera compared to 51 overall according to the counts by Robinson (1976), and so *Tabwecala robinsoni* is no exception. Besides its area, largest among the Vanuatu islands, the elevation and ecological heterogeneity (Bouchet et al. 2011), including its older age (Tennent 2004), evidently played a role in promoting endemicity in Espiritu Santo, with some taxa known only from middle to high elevation of the Tabwemasana range, e.g. *Tiracola tabwemasana* Holloway, 1979. After a study of the species assemblages across his sampling sites on this island, Robinson (1975: 76) identified a cluster of species corresponding to a "montane forest element", to which *Tabwecala robinsoni* clearly also pertains.

A review of characters of the new genus with respect to putatively related groups provided the opportunity to show that the separation of tribes Ophiusini and Poaphilini of the Erebinae is still morphologically unsubstantiated and solely based on molecular evidence, which calls for further analysis on these lineages. Poorly explored areas of the southern hemisphere such as the montane forests of Mt Tabwemasana and other major islands are likely to host representatives of other most unusual lineages of Erebidae and other Noctuoidea, which calls for the deployment of adequate measures ensuring their protection.

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